

PRINCIPAL TYPES OF VEGETATIVE SHOOT APEX ORGANIZATION IN VASCULAR PLANTS¹

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Before progress can be made in research, a problem must be recognized. Once the problem has been perceived, a research program may be directed toward a solution. The problem of how and where a shoot grows and the organization of the shoot apex was apparently first conceived by Kaspar Friedrich Wolff (1759). Although his observations on the structure, formation, and growth of cells were fantastically inaccurate, he made a great contribution to our knowledge of the growing plant by setting forth a new and important problem. In a very real sense, Wolff is the father of developmental plant anatomy.

Disagreement is the life blood of many research problems. Strenuous opposition is often engendered by a dogmatic statement or a theory which is proposed as a universal truth. Opposition to Wolff's (1759) original proposition regarding the organization and growth of shoot apices prompted plant anatomists, some 85 years later, to investigate the truth of the statement. The factual solution of the problem of shoot apex organization had its beginnings in the work of Nägeli (1845). Following this work on many lower cryptogams, Nägeli concluded that the cells of all tissues of the shoot of cryptogams and higher plants have their genesis in a single apical cell. The new-born apical cell theory supported by Hofmeister (1851) and others provided the impetus for a renewed, vigorous attack on the problem of shoot apex organization. A little later a new proposal, Hanstein's (1868) histogen theory was born of more careful observations and in a mind unfettered by the prevailing fanaticism of the apical cell theorists. The histogen theory in turn, sparked another rigorous attack (Pringsheim, 1869; Strasburger, 1872; Warming, 1872; Kny, 1878; Klercker, 1885; Groom, 1885; Dingler, 1866; Douliot, 1890; Koch, 1891, 1893; Schmidt, 1924; Foster, 1935; Korody, 1937; and others) on the problem of shoot apex organization. It would seem that Hanstein's principal contribution to the subject of shoot apex organization was his recognition (1) of the dissimilarity in structure between the shoot apices of vascular cryptogams and phanerogams and (2) that the apices of angiosperms are constituted of growth zones. More recently Schmidt (1924) proposed the tunica-corpus theory as the result of additional and more accurate observations on the structure of the angiosperm shoot apex. Schmidt accepted Hanstein's basic thesis that angiosperm shoot apices exhibit growth zones, but disagreed with the unrealistic zonal pattern suggested. Schmidt's new zonal pattern concept distinguished the two zones (tunica and corpus) by their intrinsically different manner of growth. One of the factors which accounts for the present day interest and emphasis on studies concerning the organization and growth at shoot apices is the disagreement (Majumdar, 1945; Dermen, 1947; Reeve, 1948; Popham and Chan, 1950; and others) concerning the validity and general suitability of Schmidt's terminology.

In the author's opinion sufficient observations have been made on shoot apex organization and the relation of zonal patterns to shoot growth to make a systematic summary of them worth while. It is the writer's intent to summarize and classify the accumulated information so as to present a view of the basic organizational patterns encountered to date in the shoot apices of vascular plants. In addition, it is hoped that this paper will be a unifying basis for future investigations and

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discussions concerning the organization of shoot apices. Certain inconsistencies will become apparent to the reader and it is hoped that these will provide the stimulus for further research. Whether the number of types suggested will be increased or decreased as time goes by is of little importance. Whether each plant is correctly typed will depend upon the accuracy and thoroughness of the recorded observations on that plant. It would indeed prove amazing if all of the plants herein typed were later found to be classified correctly in the light of further investigations.

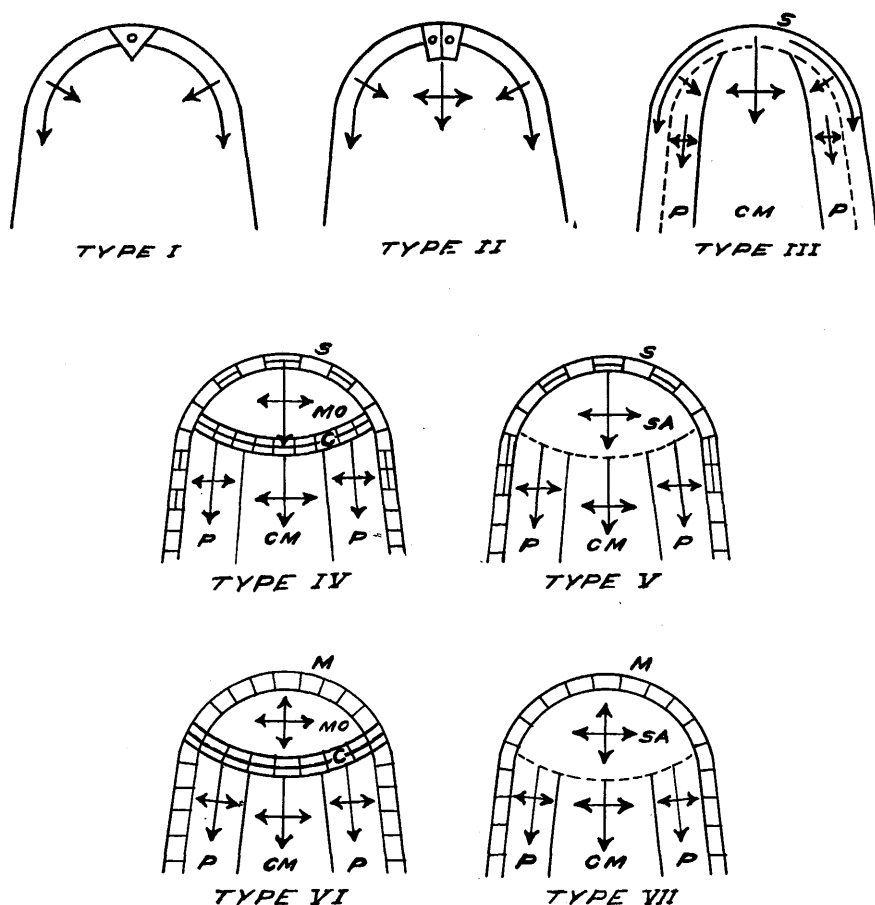


FIGURE 1. Diagrammatic representations of longisections through shoot apices illustrating the seven principal types of organization found among vascular plants. (S, surface meristem; M, mantle; MO, central mother cells; C, cambium-like zone; SA, sub-apical initials; CM, central meristem; P, peripheral meristem.)

It is not within the scope of this paper to discuss in detail the various theories of shoot apex organization. This has already been done by such able authors as Schüepp, 1926; Foster, 1939b, 1941a, 1949; Sifton, 1944; Wardlaw, 1945; Majumdar, 1945. Neither is it planned to discuss in detail the genetic, phylogenetic, and growth-form implications of each type of apical organization. These

aspects have already received the attention of numerous authors (Bower, 1889, 1890-91; Satina, Blakeslee, and Avery, 1940; Cross, 1941, 1942; Satina and Blakeslee, 1941, 1943; Dermen, 1945, 1947).

No attempt has been made to recite all of the facts reported by investigators (particularly the early investigators) whose works have been superseded by more thorough investigations and re-evaluated in the light of additional data. It has already been suggested that many of the early investigators labored during a period when only one concept of shoot apex organization (the apical cell theory) was prevalent. In addition to this limitation, the theory was supported by leading plant anatomists whose reputations as careful investigators were not to be doubted. In the light of (1) the vigorous support accorded the single theory of shoot apex organization, (2) poor microtechniques, and (3) poor optical equipment, it is remarkable that so many of the data obtained by the earlier workers have stood the acid test of reinvestigation.

Based on the facts now available, shoot apices of vascular plants may be grouped, with reference to differences in their cellular organization, into seven distinct categories (fig. 1).

TYPE I. FERN TYPE

In the first of these categories may be placed a group of pteridophytes having a *single apical cell* located at the summit of the shoot apex. The apical cell may be two-sided (three faced), both sides being convex, or it may be an inverted three- or four-sided (four or five faced) pyramidal cell. In any case the single apical cell occupies the summit position of the shoot apex and is the forerunner of all of the cells in the shoot apex. New cells are formed from the apical cell by a regular sequence of divisions in which the new cell walls lie parallel to the side walls of the apical cell. Each division of the apical cell results in two dissimilar cells, one of which enlarges and assumes the characteristic features and size of the original apical cell. Anticlinal and then periclinal cell divisions occur subsequently in the other cell newly formed from the initial. The cells thus formed later differentiate into the tissues of the shoot. No cell walls form parallel to the "base" of the initial, which lies at the surface of the shoot apex. For this reason the apical cell remains at the summit, with one surface exposed to the atmosphere.

Some of the plants which have shoot apices belonging to Type I are listed below.

<i>Niphobolus chinensis</i>	Apical Cell with two convex sides	(Hofmeister, 1862)
<i>N. rupestris</i>	"	" "
<i>Selaginella hortensis</i>	"	" "
<i>S. galeotii</i>	"	" "
<i>S. martensii</i>	"	(Pfeffer, 1871; de Bary, 1884)
<i>S. umbrosa</i>	"	(Wand, 1914)
<i>Azolla</i> sp.	"	(de Bary, 1884)
<i>Salvinia natans</i>	"	(de Bary, 1884; Zawidzki, 1912)
<i>Pteris aquilina</i>	"	(de Bary, 1884; Chang, 1927)
<i>Polypodium rupestre</i>	"	(de Bary, 1884)
<i>P. lingua</i>	"	" "
<i>P. aureum</i>	"	" "
<i>P. punctatum</i>	"	" "
<i>P. phymatodes</i>	"	" "
<i>Platyserium alciorne</i>	"	" "
<i>Pteridium</i> sp.	"	(Bower, 1923)
<i>Nephrolepis undulata</i>	Biconvex or three-sided pyramidal apical cell	(de Bary, 1884)
<i>Polypodium vulgare</i>	"	" "

<i>Equisetum arvense</i>	Three-sided (tetrahedral pyramidal apical cell	(Cramer, 1855)
<i>E. limosum</i>	"	(Reess, 1867)
<i>E. hiemale</i>	"	" "
<i>E. variegatum</i>	"	" "
<i>E. palustre</i>	"	(Vidal, 1912)
<i>E. scirpoides</i>	"	(Johnson, 1933)
<i>Ophioglossum vulgatum</i>	"	(Hofmeister, 1857)
<i>Marsilea vestita</i>	"	(Hanstein, 1865-66; Campbell, 1905)
<i>Psilotum triquetrum</i>	"	(Solms-Laubach, 1884; Ford, 1904)
<i>Pilularia</i> sp.	"	(Bower, 1889)
<i>Amphicosmia walkerae</i>	"	" "
<i>Ceratopteris</i> sp.	"	" "
<i>Hymenophyllaceae</i>	"	" "
<i>Lygodium scandens</i>	"	" "
<i>Aneimia hirta</i>	"	" "
<i>Tmesipteris</i> sp.	"	(Holloway, 1917, 1921)
<i>Osmunda cinnamomea</i>	"	(Cross, 1931)
<i>Selaginella wildenovii</i>	"	(Barclay, 1931)
<i>S. sinensis</i>	"	(Hsü, 1937)

Selaginella martensii (Treub, 1876) is an interesting example of a plant with a variable Type I organization. The sporeling stages show a four-sided pyramidal cell at the shoot apex while older plants have a three-sided pyramidal cell or an apical cell with two convex sides. The same sequence of events has been observed for lateral shoot apices as well as for principal shoot apices.

TYPE II. TRANSITION TYPE (TENTATIVE)

The second category includes a group of pteridophytes whose shoot apices exhibit *two to five apical cells* (fig. 1). These initials usually prismatic in form, not pyramidal, divide anticlinally and occasionally periclinally. The new cell walls lie parallel to the side walls and the sub-surface end wall of prismatic cells. No new cell walls form near the exposed surface of the cells. For this reason the apical cells remain at the summit of the shoot apex. Subsequently the new cells divided anticlinally and periclinally. From these cells the tissues of the shoot differentiate.

A great deal of care must be exercised in interpreting the structure of shoot apices of the pteridophytes in which one or more apical initials are thought to exist. Williams (1931) and others have clearly shown that a median longisection may reveal one large apical cell appearing triangular in form while in a median longisection taken at right angles to the first, one may see two narrow, more or less prismatic apical cells. In addition, if shoot apices in the early stages of branching are observed, 2, 4, or more cells representing two sets of adjacent apical initials of two incipient branches may be seen. In either of the cases cited above, a misconception of the structure of the shoot apex might be obtained.

The comments of authors and their illustrations, at least in some cases, indicate that well defined apical cells do not exist. Instead the shoot apex is covered with an unstratified row of periclinally and anticlinally dividing cells some of which nearest the summit may be slightly larger than those on the flanks. It might be expected, therefore, that species segregated into this category on the basis of present evidence may, later, upon re-examination of the evidence, be placed under Type III.

Plants which have been reported to exhibit this type of shoot apex organization are listed below.

<i>Selaginella wallichii</i>	2 apical initial cells (four-sided pyramids)	(Strasburger, 1873)
<i>S. grandis</i>	2 apical initial cells	(Williams, 1931)
<i>Marattia fraxinea</i>	4 or more apical initial cells	(Bower, 1889)

Selaginella kraussiana (Wand, 1914) exhibits both Type I and Type II organization in the same plant and therefore, in a sense, represents a transitional form. The main shoot reportedly has two four-sided pyramidal cells at the shoot apex while the side shoots have only one three-sided pyramidal cell at the apex.

TYPE III. LYCOPODIUM TYPE

The species (pteridophytes, with one exception) belonging to this category have shoot apices which exhibit three zones (fig. 1). Zone 1, the surface meristem, is an *unstratified* surface cloak of cells dividing by anticlinal, periclinal, and slanting walls. The cells differ in size, shape, and dimensions. In a median longisection the surface cap of cells appears very irregular due to the fact that some cells are short, just having divided periclinally; some are triangular, the result of a spindle oriented obliquely; some are long and slender; and some are long and broad. In many² species, periclinal divisions are more frequent than anticlinal or oblique divisions. This seems to be the principal factor responsible for the extreme irregularity of the outer row of cells. The cells are not uniform and do not form a clearly stratified layer such as will be found in Types IV to VII.

No apical cell or *distinct* group of initial cells are distinguishable from the other cells of the surface cloak. Foster (1939a) as well as Härtel (1938) have chosen to refer to a central terminal group of cells in shoot apices of seedlings (but not in older plants) of *Cycas revoluta* and in old plants of *Lycopodium* spp. as "apical initials." The descriptions and photomicrographs of both authors clearly indicate that these "apical initials" of the surface cloak exhibit no differences in size, shape, and plane of cell division from those of other cells of the surface cloak. Periclinal divisions occur throughout the surface cloak of cells. It seems to the author that these "apical initials" differing from other cells of the surface cloak in one respect only, i.e., location, do not constitute a separate and distinguishable growth zone. The group of cells might logically be termed *apical* because of its location. The term "apical initials," however, would seem to imply (1) a group of cells showing a distinctive "fixed or regular scheme of segmentation" and (2) a group of cells ultimately responsible for the initiation of all cells of the shoot apex. The "apical initials" of *Cycas revoluta* seedlings (Foster, 1939a) and *Lycopodium* spp. old plants (Härtel, 1938) are not distinctly different from any other cells of the surface cloak in either respect. Foster (1940) admittedly found no evidence for a group of "apical initials" in shoot apices of older plants of *Cycas revoluta*.

The cells of Zone 1 act as the initials of (1) the epidermis, (2) zone 2, and (3) indirectly as initials of all other tissues of the shoot apex. Zone 1 is of paramount importance in determining the growth of the shoot as a whole.

Under the central portion of the surface meristem lies Zone 2, the *central meristem*. At the irregular and indefinite junction of the two zones, periclinal derivatives lie in vertical tiers under the surface cells. The basal cells of the tiers divide by periclinal, anticlinal, and slanting walls resulting in a mass of irregularly arranged cells. Occasionally some of these cells and their derivatives divide transversely a number of times resulting in short chains of cells as might be expected in a rib meristem. Most of the enlarging cells of the zone become highly vacuolate and account for rapid growth in diameter very close to the shoot tip. Cells of Zone 2 differentiate into the central tissues of the shoot, i.e., in *Cycas revoluta*, the pith; in *Lycopodium*, the stele.

Zone 3, the peripheral meristem flanks the central meristem. It derives new cells from three sources (1) from periclinally dividing surface cells on the flanks of the apex, (2) from anticlinal, periclinal, and oblique divisions of cells within the zone itself, and (3) in some instances (as in *Cycas revoluta*) from anticlinal

²The careful investigations of West and Takeda (1915) on several species of *Isoetes* indicates that cells of the surface cloak divide periclinally only occasionally, while in the underlying mass of cells, periclinal and anticlinal divisions occur in equal numbers.

and oblique cell divisions at the periphery of Zone 2. The cells of the peripheral meristem are ordinarily smaller than those of Zone 2 and are often elongate. Out of the cells of the zone differentiate the cortex and, in *Cycas revoluta*, the procambium and leaf primordia. In *Lycopodium* and *Selaginella*, leaf primordia originate in Zone 1.

Some of the plants whose shoot apices exhibit Type III organization are the following:

<i>Lycopodium selago</i>	(Cramer, 1855; Strasburger, 1872; Härtel, 1938)
<i>L. lucidulum</i>	(Turner, 1924)
<i>L. complanatum</i>	(Härtel, 1938)
<i>L. alpinum</i>	" "
<i>L. annotinum</i>	" "
<i>Selaginella arborescens</i>	(de Bary, 1884)
<i>S. pervillei</i>	" "
<i>S. spinulosa</i>	(Bruchmann, 1897)
<i>S. lyallii</i>	(Bruchmann, 1909a, 1910)
<i>S. preissiana</i>	" " "
<i>S. lepidophylla</i>	(Wand, 1914)
<i>S. uncinata</i>	" "
<i>S. oregana</i>	(Smith, 1938)
<i>Isoetes duriæi</i>	(Hegelmaier, 1874)
<i>I. japonica</i>	(West and Takeda, 1915)
<i>I. lacustris</i>	(West and Takeda, 1915; Bruchmann, 1874; Farmer, 1890-91)
<i>I. hystrix</i>	(West and Takeda, 1915)
<i>I. velata</i>	(West and Takeda, 1915; Hegelmaier, 1874)
<i>Phylloglossum</i> sp.	(Bower, 1886)
<i>Macroglossum alidae</i>	(Campbell, 1914)
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<i>Cycas revoluta</i>	(Foster, 1939a, 1940)

West and Takeda (1915) assert that even the youngest plants of the *Isoetes* species which they have studied have a shoot apex organization like Type III. Bruchmann (1874) and Farmer (1890-91) working with *Isoetes lacustris* and Hegelmaier (1874) working with *Isoetes velata* and *Isoetes duriæi* reached the same conclusion. These data are in disagreement with the earlier works of Hofmeister (1862) on *Isoetes lacustris* in which he reported a single tetrahedral cell. The age of the plant examined by Hofmeister was not stated. Scott and Hill (1900) working with young specimens of *Isoetes hystrix* reported finding a single prismatic several-sided apical cell which was somewhat larger and longer than other unstratified cells of the surface layer. For shoot apices of older plants they reported two somewhat larger apical cells. In the oldest specimens they found an unstratified layer of many cells (Type III).

A great deal of discussion and research has centered about the problem of shoot apex organization of the species belonging to the Marattiaceae. Many differences of opinion held by various workers have now been resolved by investigators who have studied plants of the same species at different ages. It now appears that a single apical cell is usually found in the shoot apex of the young sporeling. In somewhat older plants, this apical cell is no longer evident but instead, a group of equivalent initial cells or an unstratified layer of cells becomes apparent. In *Danaea alata*, *Danaea nodosa*, and *Kaulfussia aesculifolia* (West, 1917) the young sporeling has a single three-sided pyramidal or prismatic apical cell, the older sporeling has a single four-sided more or less prismatic apical cell while rapidly growing older stems exhibit an unstratified layer of many cells dividing both anticlinally and periclinally (Type III). The same series of events occurs in *Danaea simplicifolia* (Brebner, 1896, 1901, 1902) except that the single apical cell of the

young sporophyte is four-sided. A three-sided prismatic or a wedge-shaped cell occurs in the shoot apex of the young sporophyte of *Angiopteris evecta* (Bower, 1885, 1889; Farmer and Hill, 1902) while an unstratified layer of equivalent initials appears in the shoot apex of rapidly growing older plants. Jonkman (1896, 1897) reported finding an unstratified layer of cells over the shoot apex surfaces of very young and older sporophytes of both *Angiopteris* and *Marattia* species. Charles (1911) found a single apical initial cell (at first three-sided and pyramidal, then four-sided and prismatic) in the sporophyte shoot apex of *Marattia alata* while an unstratified surface layer of cells covered the shoot apices of older plants (Type III).

Some species of the genus *Selaginella* exhibit variations worthy of note. Burchmann (1909b) described the young shoot apex of *Selaginella poulleri* as having a three-sided pyramidal cell (Type I) while shoot apices of older branches have several initial cells arranged in an unstratified layer (Type II or III). According to Wand (1914) *Selaginella gracilis* exhibits Type III organization in the main shoot apices. Side branches of the same plants at first have two four-sided cells at the summit of the shoot apex and later have one apical cell with two convex sides.

At the shoot apex of *Lycopodium phlegmaria*, Treub (1886) found one prismatic initial cell in very young plantlets, two in older plantlets, and his figures illustrate an unstratified layer of six to twelve cells (Type III) in still older plants.

TYPE IV. GINKGO TYPE

The Type IV shoot apex organization is characterized by five zones (fig. 1). Zone 1, the *surface meristem*, consists of a rather well defined surface layer of cells or, as in *Dioon edule* (Foster, 1941b), *Microcycas calocoma* (Foster, 1943), *Zamia* spp. (Johnson, 1939), and others, a surface layer of cells and their periclinal derivatives arranged in more or less well defined vertical tiers. In *Zamia*, additional tiers may be initiated by the anticlinal or oblique division of any cell of the tier. When this occurs, the regularity of the tier pattern is somewhat altered. Cells of the surface layer may be more or less the same size, or as in *Ginkgo* and *Sequoia*, there may be a small number of larger periclinally dividing "apical initial cells" at the summit of the apex. Since most of the cell divisions are anticlinal, the layer in most instances appears more or less discrete. Some periclinal divisions do occur in both the summit and flank cells of the surface layer. Although they are relatively infrequent, they are probably more abundant at the summit in the group of "apical initial cells." The surface layer of cells therefore not only perpetuates itself but contributes cells to the zones lying beneath. Because of these periclinal divisions, the surface row of cells should not be termed a protoderm.

Zone 2, a group of *central mother cells*, lies in a central position directly below Zone 1 and lacks the characteristics associated with meristems of spermatophytes. The irregularly arranged polygonal cells of the zone are larger, sometimes very much larger, than any of the surrounding cells. They may have huge nuclei, much-vacuolated cytoplasm, and often much-thickened walls, particularly at the cell corners. It may be inferred from their large size that cell division is relatively infrequent, cell enlargement being the more characteristic process. This group of cells, lenticular in *Ginkgo* and others, or funnel-shaped in *Microcycas* and others, is maintained during shoot elongation (1) by periclinal divisions and subsequent enlargement of the innermost cells of Zone 1 and (2) by infrequent cell divisions which occur in diverse planes in the central mother cells. Zone 2 is primarily a region of increase in volume.

Zone 3, a *cambium-like zone* of tabular cells, forms a cup-shaped transition region between Zone 2 and the zones lying below. The rather narrow zone is characterized by relatively frequent cell divisions in planes at right angles to radii centering at the summit of the apex. Some cell divisions occur parallel to the radii. The zone, therefore, perpetuates itself in thickness and diameter and contributes cells to the zones lying beneath it.

Zone 4, the *central meristem*, constituted of pith initials or rib meristem or both, lies directly below the central portion of the cup-shaped zone of cambium-like cells. The zone consists of (1) a large number of cells which are produced by continued transverse divisions and (2) a smaller number of cells dividing in other planes. As a result, the cells are more frequently arranged in continuous rows or several-celled chains which are tapered at both ends. Cell elongation and enlargement are rapid. Cell divisions in Zone 3 and within Zone 4 itself perpetuate the meristem. Pith differentiates from the rib meristem or directly from pith initials.

Zone 5, the *peripheral meristem*, forms a cylinder lying subjacent to the edge of the cup-shaped or funnel-shaped Zone 3. The meristem is perpetuated by cells contributed by Zones 1 and 3 and by periclinal and anticlinal cell divisions within the peripheral meristem. The epidermis, cortex, foliar primordia, procambial ring and in some cases, as in *Zamia* and *Microcycas*, the outer pith cells differentiate from the cells of Zone 5.

It will be seen from the foregoing that Type IV differs in a very important manner from Types I, II, and III. Even though cells of the surface layer divide periclinally in Type IV shoot apices, they are relatively indirect in their contribution to extension growth of the central and peripheral meristems while periclinally dividing surface cells of Types I, II, and III are of prime and direct importance in this respect.

Some of the species having Type IV shoot apex organization are listed below.

<i>Ginkgo biloba</i>	(Foster, 1938)
<i>Zamia integrifolia</i>	(Johnson, 1939)
<i>Z. silvicola</i>	" "
<i>Z. umbrosa</i>	" "
<i>Z. umbrosa</i>	" "
<i>Z. latifoliata</i>	(Johnson, 1945)
<i>Dioon edule</i>	(Foster, 1941b)
<i>Microcycas calocoma</i>	(Foster, 1943)
<i>Encephalartos villosus</i>	(Johnson, 1944)
<i>E. woodii</i>	" "
<i>E. horridus</i>	" "
<i>E. lehmanii</i>	" "
<i>E. frederici-guilielmi</i>	" "
<i>E. altensteinii</i>	" "
<i>Bowenia serrulata</i>	" "
<i>Macrozamia spiralis</i>	" "
<i>M. corallipes</i>	" "
<i>Sequoia sempervirens</i> ³	(Sterling, 1945; Cross, 1943b)
<i>Pseudotsuga taxifolia</i>	(Allen, 1947; Sterling, 1946)

TYPE V. ABIES-CRYPTOMERIA TYPE

Shoot apices in this category exhibit four growth zones (fig. 1). Zone 1, the *surface meristem*, is a well defined layer of cells apparently uniform in thickness. Anticlinal divisions predominate in the layer but periclinal divisions occur more than occasionally. Periclinal divisions may (1) be limited to or near the summit, except at loci of leaf and bud initiation (refer to list B below) or (2) may occur at any locus in the surface layer (refer to list A below). It seems to the author that periclinally dividing cells located only at the summit in the surface layer may justifiably be referred to as "apical initials." This has been done by Cross (1939, 1941, 1942, 1943a, 1943b). However, the application of the term "apical initials"

³Type IV organization is present in apices of leading shoots while Type V organization occurs in apices of lateral branches (Sterling, 1945).

to the central cells of the surface layer appears indefensible if any or all of the morphologically similar cells of the surface layer may be expected to contribute to underlying zones. Some workers have done this. In either case, periclinal divisions appear to be either infrequent or quickly followed by (1) cell enlargement or (2) anticlinal cell divisions. Evidence for this statement is the stratified appearance of the surface layer. The periclinally dividing cells contribute to Zone 2 and thus help to perpetuate it. Frequent anticlinal divisions occur in the surface layer both at the summit and along the flanks and account for the extension growth of the cell layer destined to differentiate into epidermis. While the cells of the surface layer may vary greatly in size, reports by early workers of an "apical cell" have not been confirmed by recent investigators.

It should be understood that periclinal division spindles or evidence of periclinal divisions are not always found in the surface layer of every median section of comparable shoot apices of each individual plant. However, the percentage of apices exhibiting the phenomenon is sufficiently high to eliminate the probability that the periclinal divisions are rare or chance occurrences, except possibly in *Ephedra*, *Gnetum*, and the permanent shoots of *Taxodium*. There is some evidence to support the claim that periclinal divisions occur in the surface layer of shoot apices more frequently at the time of elongation of the shoot (Gifford, 1943; Kemp, 1943).

In Zone 2, a group of *sub-apical initials*, vertical and oblique divisions occur but horizontal divisions are probably more common. The cells may be few in number (in small apices) and may be arranged irregularly or in short tiers. They are mostly larger but less vacuolate than the neighboring cells. The zone is not clearly demarcated in all apices. Zone 2 is perpetuated not only by internal cell divisions but by periclinal divisions in the central cells of the surface meristem. Cell divisions on the periphery of the zone account for growth in length of Zone 4, while basal derivatives of the zone contribute to the growth in length of Zone 3.

Zone 3, the *central meristem*, differentiates directly from the sub-apical initials, there being no intervening zone of cambium-like cells. Cells of the central meristem divide most frequently in a transverse plane and often are arranged in short tapered chains and irregular vertical rows. Cells thus formed, as well as those contributed by transverse divisions of the central marginal cells of Zone 2, account for growth in length of the rib meristem. The highly vacuolate, enlarging cells of the rib meristem differentiate into pith.

Zone 4, the *peripheral meristem*, forms a cylinder of elongating and dividing cells surrounding Zone 3. Divisions occur in various planes but the cells often appear to be arranged in ill-defined layers due to a higher frequency of anticlinal (with reference to the flanks) divisions. The cells later differentiate into procambial and cortical tissues and are responsible for initiation of lateral organs. In some species new cells are contributed to the zone as the result of periclinal divisions along the flanks of the surface meristem. In some species Zones 3 and 4 appear quite distinct, while in others (as in *Cunninghamia*) derivatives of marginal cells of the rib meristem augment the peripheral meristem zone.

Species having Type V shoot apex organization are listed below.

A. Periclinal divisions occur at the summit and along the flanks in the surface layer.

<i>Pinus canadensis</i>	(Groom, 1885)
<i>P. sylvestris</i>	" "
<i>P. montana</i>	(Korody, 1937)
<i>Abies pectinata</i>	(Groom, 1885)
<i>A. alba</i>	(Koch, 1891)
<i>A. concolor</i>	(Korody, 1937)
<i>A. venusta</i>	(Foster, 1941a)

<i>Taxus baccata</i>	(Koch, 1891)
<i>T. canadensis</i>	" "
<i>Picea excelsa</i>	(Koch, 1891; Korody, 1937)
<i>P. orientalis</i>	(Koch, 1891)
<i>Torreya californica</i>	(Kemp, 1943)
<i>Metasequoia glyptrostroboides</i>	(Sterling, 1949a)
<i>Gnetum gnemon</i> ⁴	(Johnson, 1950)
B. Periclinal divisions in the surface layer occur at the summit only.	
<i>Ephedra campylopoda</i>	(Strasburger, 1872)
<i>E. altissima</i>	(Koch, 1891; Gifford, 1943)
<i>Cephalotaxus pedunculata</i> ⁵	(Koch, 1891)
<i>Juniperus communis</i> ⁵	" "
<i>Cedrus libani</i> ⁵	" "
<i>Larix decidua</i> ⁵	" "
<i>Tsuga canadensis</i> ⁵	" "
<i>Pinus strobus</i> ⁵	" "
<i>Taxodium distichum</i> ⁶	(Cross, 1939)
<i>Cryptomeria japonica</i>	(Cross, 1941)
<i>Cunninghamia lanceolata</i>	(Cross, 1942)
<i>Taiwania cryptomerioides</i>	(Cross, 1943a)
<i>Sequoia gigantea</i>	(Cross, 1943b)
<i>Athrotaxis selaginoides</i>	(Cross, 1943a)

The reader will note that *Sequoia sempervirens* was listed among those plants exhibiting Type IV shoot apex organization while *Sequoia gigantea* has been described as having Type V shoot apex organization. The two types differ principally in the presence (Type IV) or absence (Type V) of a cambium-like zone. It has been shown for *Chrysanthemum* (Popham and Chan, 1950) that the presence of a cambium-like zone occurs in the mid-phase and is absent in the late-phase of the plastochrone. One might speculate therefore that a re-examination of *Sequoia gigantea* shoot apices would yield similar information. Sterling (1945) suggested another possible explanation for this incongruity in his statement that "Cross' description of the leading shoot apex of *Sequoia (gigantea)* seems to correspond to the writer's observations on the apices of lateral branches."

TYPE VI. THE OPUNTIA TYPE

The Opuntia Type of shoot apex organization, occurring in angiosperms only, consists of 5 zones (fig. 1). Zone 1, the *mantle*, forms a cap of one or more discrete layers of cells over the summit. In at least the surface layer, cell divisions are of one type only—anticlinal. If more than one layer of cells is present, anticlinal divisions occur exclusively or predominantly in them. In species having a several-layered mantle, successive underlying layers often exhibit a progression from exclusively anticlinal divisions in the surface layer or layers toward more frequent periclinal divisions (Popham and Chan, 1950). In the author's opinion, the term *tunica*, if used, should refer only to those surface layers in which *only* anticlinal

⁴Periclinal divisions in the surface layer of cells are apparently located on the flanks of the apex only, above the position of leaf initiation.

⁵Although Koch's descriptions of the shoot apices of these species are not at all clear, it seems reasonably certain that the species should be listed as having Type V organization. Koch is vague as to whether periclinal divisions occur at the summit in the surface layer or both at the summit and along the flanks. Shoot apices of these species should certainly be re-investigated.

⁶Type V organization is present in shoot apices of most deciduous shoots while Type VII organization occurs in the primordial stages of all shoots and during the expansion phases of most permanent shoots (Cross, 1939).

divisions occur (Popham and Chan, 1950). The term will be so used in this paper. The tunica, therefore, perpetuates (1) itself, (2) the epidermis of the shoot, and (3) may, if more than one layer of tunica is present, contribute to the zone of cambium-like cells (Zone 3). The tunica is an independent histogen only when it consists solely of one layer of cells. The cells of the surface layer, when viewed in longisection, are very nearly equal in thickness although the summit cells of the layer may be vacuolate, very much wider, and somewhat more irregular in thickness than the cells on the flanks. This combination of characteristics suggests the probability that cell divisions are less frequent at the summit than on the flanks.

Zone 2, the *central mother cells*, is composed of a relatively small number of large, closely appressed, irregularly shaped, often conspicuously vacuolate cells. Cell walls in some species are quite thick, particularly at the corners. Cell divisions may occur in many different planes, but at relatively infrequent intervals. Since the mantle (Zone 1) may include some sub-surface layers of cells in which periclinal divisions occur less or more frequently, Zone 2 may receive cellular contributions from the innermost of the mantle layers. In species such as *Trichocereus* and *Opuntia* in which only one mantle layer (a tunica layer) occurs, Zone 2 perpetuates itself independently and is truly a zone of initiation for the entire shoot, except the epidermis. Transverse and obliquely dividing cells along the inner boundary of the zone contribute new cells to Zone 3.

Zone 3, the *cambium-like zone*, is more or less cup-shaped, underlies Zone 2, and extends to the perimeter of the shoot tip. Its cells are meristematic, their protoplasm is dense, and their shape is reminiscent of stelar cambium cells. Most cell divisions are in planes at right angles to radii centering at the summit of the apex. The cells are frequently elongated paralleling the arc of the zone. New cells are contributed to Zone 3 by Zone 2 and in some species in which the cambium-like zone interrupts the surface layer (as in *Chrysanthemum*), by both Zones 1 and 2. The zone may be only a few tiers of cells thick and therefore indistinct, or it may be well defined, 8-10 cells deep, (as in *Trichocereus*). Cells formed in Zone 3 lie in longitudinal rows and account for growth in length of Zones 4 and 5.

Zone 4, the *central meristem*, originates from transverse divisions in the central cells of the zone of cambium-like cells (Zone 3). Transverse divisions predominate in the zone, resulting in the formation of tapering strands of mitotically related cells and irregular tiers of cells. Newly formed cells elongate and enlarge rapidly as evidenced by their large vacuoles. The cells differentiate into pith only (as in *Opuntia* and *Chrysanthemum*) or into pith and medullary procambial strands (as in *Phoenix* and *Trichocereus*).

Zone 5, the *peripheral meristem*, forms a cylinder lying within the protoderm and around the central core of cells (Zone 4). Cells of the zone are usually much smaller than those of Zone 4 and are mostly elongated axially. They divide both anticlinally and periclinally. Transverse divisions predominate resulting in a tissue whose cells appear somewhat stratified. Vacuolation of most cells, especially those lying closest to Zone 3, is slight. The zone gives rise to the cortex, foliar organs, and all (as in *Opuntia* and *Chrysanthemum*) or a part (as in *Phoenix* and *Trichocereus*) of the procambial tissue.

Some of the species exhibiting Type VI shoot apex organization are the following.

Number of Mantle Layers

<i>Livistona chinensis</i>	2	(Helm, 1936)
<i>Phoenix canariensis</i>	1	(Ball, 1941)
<i>P. dactylifera</i>	1	(Ball, 1941)
<hr/>		
<i>Trichocereus spachianus</i>	1	(Boke, 1941)
<i>Opuntia cylindrica</i>	1	(Boke, 1941)
<i>Bellis perennis</i>	2	(Philipson, 1946)

<i>Liriodendron tulipifera</i>	2-3	(Millington and Gunckel, 1950)
<i>Chrysanthemum morifolium</i> ⁷	2-5	(Popham and Chan, 1950)

TYPE VII. THE USUAL ANGIOSPERM TYPE

The Usual Angiosperm Type of shoot apex organization, occurring in angiosperms only, with two doubtful exceptions, is characterized by 4 zones (fig. 1). Zone 1, the *mantle*, consists of at least one discrete, independent, and self-perpetuating surface layer whose cells divide *exclusively* in anticlinal planes. The mantle may consist (1) solely of the one tunica layer or (2) of one (usually), two, or more tunica layers plus one or more sub-tunica layers of cells in which periclinal and occasionally oblique divisions occur, but in which most divisions are anticlinal. The total number of cell layers in the mantle varies from one to nine. Shoot apices of angiosperms reportedly exhibiting isolated instances of periclinal divisions in the surface layer such as *Zea mays* (Sharman, 1940), *Agropyron repens* (Sharman, 1943), *Chlorogalum pomeridianum* (Sterling, 1944), *Ruppia maritima* and *Cymodocea nodosa* (Pottier, 1934), *Triticum vulgare* (Rösler, 1928), and *Avena sativa* (Kliem, 1937) are for the present considered unusual irregularities and the species, for which sufficient additional data are available, are included in Type VII. If it can be demonstrated that periclinal divisions occur in the surface layer with any degree of regularity, the apex should be classified as Type V. Periclinal divisions when present in cells of the inner mantle layers result in cellular additions to Zone 2. In median longisections, cells of the surface tunica layer (and usually in other tunica layers if present) appear to be uniform in thickness even though those at the summit may be larger (wider) than those on the flanks.

Reeve's (1948) suggestion that generally the number of mantle layers observed in a shoot apex is less following leaf initiation than immediately preceding leaf initiation has been supported by Sterling (1949b) and Cross (1937). This proposition has been challenged by Popham and Chan (1950), Millington and Gunckel (1950), and others.

Zone 2, the *sub-apical initials*, is composed of a self-perpetuating group of irregularly shaped cells which may divide in various planes. The rate of cell division is relatively slow in the lenticular zone of sub-apical initials when compared with the rate in the surrounding zones. The cells of Zone 2, located at the summit of the apex back of the mantle, are usually larger, often highly vacuolate, and therefore lighter staining, than surrounding cells. Strictly speaking, periclinally dividing central cells of inner mantle layers should also be included as sub-apical initials. Sub-apical initials of *lateral* shoots in *Succisa* (Philipson, 1947) apices are exceptional in that they apparently are smaller, not larger, than surrounding cells. In some species (as in *Sinocalamus beecheyana*) cell walls are thickened, particularly at the corners. The zone may consist of many cells in the larger apices or as few as one single cell in the narrow apices of slender grasses (Sharman, 1945). Cross (1937) reported that "the initials of *Viburnum rufidulum* gradually lose their identity and often may not be seen at all prior to the initiation of a pair of leaves." A condition, first reported by Ball (1949) for *Lupinus albus* in which sub-apical initial cells divide forming individual groups of cells surrounded by the original cell wall, is apparently an infrequently encountered phenomenon of Zone 2. Since the zone is the forerunner of Zones 3 and 4 it is in many species the ultimate origin of all tissues of the shoot apex except the epidermis and its derivatives.

Zone 3, the *central meristem*, lies in the central part of the apex immediately below Zone 2. The zone enlarges by (1) contributions of cells from Zone 2, (2) by divisions (mostly transverse) of central meristem cells themselves, and (3) by cell enlargement and cell elongation. Due to successive transverse divisions of central

⁷The *Opuntia* Type of organization is present during the early and mid phases of the plastochrone while the Usual Angiosperm Type of organization (Type VII) is apparent in the late phase of the plastochrone.

meristem cells, tapering files and irregular tiers result in the formation of a rib meristem. The rib meristem is not a constant feature of the zone in all species but is usually present in larger apices. Cells of the zone differentiate into pith or into pith and medullary procambial strands. The cells are usually highly vacuolated and therefore light-staining. Primary pit fields are commonly found on the cell walls.

Zone 4, the *peripheral meristem*, forms a cylinder lying beneath the protoderm and surrounding Zone 3. It grows by means of cells contributed to it (1) by Zone 1 in species having more than one mantle layer, (2) by Zone 2 and (3) by cell divisions, mostly transverse, which occur in the cells of the meristem itself. Since anticlinal (with reference to the flanks) divisions are most common, the relatively small cells of the zone become somewhat stratified. Vacuolation of the cells is usually inconspicuous, and consequently the cells stain more deeply than those in Zone 2. In most species, some cells of the zone become involved in foliar initiation while others differentiate into cortex and procambial strands.

Zones 3 and 4 are sometimes (1) indistinct as separate entities or (2) non-existent, especially in the shoot apices of monocots, particularly so in the small shoot apices of the Gramineae. Zone 4 may be reduced to a single layer of cells.

Some of the species exhibiting a Type VII zonation pattern are the following.

Number of Mantle Layers		
<i>Araucaria brasiliana</i>	3	(Strasburger, 1872)
<i>Sciadopitys verticillata</i>	2	" "
<hr/>		
<i>Elodea canadensis</i>	2	(Herrig, 1915)
<i>E. densa</i>	2	" "
<i>Hippuris vulgaris</i>	4-6	(Groom, 1885; Herrig, 1915; Louis, 1935)
<i>Dactylis glomerata</i>	1-2	(Bugnon, 1924)
<i>Melica altissima</i>	1-2	" "
<i>Secale cereale</i>	1	(Rösler, 1928)
<i>Triticum vulgare</i>	1	" "
<i>Phyllostachys nigra</i>	3	(Porterfield, 1929-30)
<i>Ruppia maritima</i>	2	(Pottier, 1934)
<i>Cymodocea nodosa</i>	2	" "
<i>Posidonia ponticum</i>	2	" "
<i>Avena sativa</i>	1	(Kliem, 1937; Hamilton, 1948)
<i>Washingtonia filifera</i>	2	(Ball, 1941)
<i>Trachycarpus excelsa</i>	2	" "
<i>Zea mays</i>	1	(Sharman, 1942)
<i>Sinocalamus beecheyana</i>	1-3	(Hsü, 1944)
<i>Agropyron repens</i>	2	(Sharman, 1945)
<hr/>		
<i>Myriophyllum spicatum</i>	2	(Groom, 1885)
<i>Ceratophyllum demersum</i>	2	" "
<i>Utricularia minor</i>	2	" "
<i>Galium rubioides</i>	2	(Herrig, 1915)
<i>Honckenya peploides</i>	3	" "
<i>Oenothera albiflava</i>	2-3	(Krumbholz, 1925)
<i>Pelargonium zonale</i>	2-4	" "
<i>Plectranthus fruticosus</i>	2-3	(Schwarz, 1927)
<i>Ligustrum vulgare</i>	3-4	" "
<i>Hypericum uralum</i>	4	(Zimmerman, 1928)
<i>Carya cordiformis</i>	2	(Langdon, 1931)
<i>C. buckleyi</i>	2-4	(Foster, 1935)
<i>Syringa vulgaris</i>	2	(Louis, 1935; Schmidt, 1924)

<i>Centaurium umbellatum</i>	2	(Halmai, 1935)
<i>Morus alba</i>	2	(Cross, 1936)
<i>Rhododendron ponticum</i>	2-4	(Foster, 1937)
<i>Viburnum rufidulum</i>	4	(Cross, 1937)
<i>Lathyrus latifolius</i>	1-3	(Schüepf, 1938)
<i>Geum urbanum</i>	2 (?)	(Grégoire, 1938)
<i>Aconitum napellus</i>	1 (?)	" "
<i>Frasera carolinensis</i>	2	(McCoy, 1940)
<i>Acacia longifolia</i> and other spp.	3-5	(Boke, 1940)
<i>Amygdalus communis</i>	4	(Brooks, 1940)
<i>Vinca rosea</i>	2-4	(Cross and Johnson, 1941; Boke, 1947)
<i>Datura stramonium</i>	3	(Satina and Blakeslee, 1941)
<i>Heracleum sphondylium</i> ⁸	8-9	(Majumdar, 1942)
<i>Garrya elliptica</i>	1-3	(Reeve, 1942)
<i>Rubus idaeus</i>	3	(Engard, 1944)
<i>R. pubescens</i>	3	" "
<i>R. rosaefolius</i>	3	" "
<i>R. hawaiiensis</i>	2	" "
<i>Descurainia pinnata</i>	2-3	(Dittmer and Spensley, 1947)
<i>Valeriana officinalis</i>	1	(Philipson, 1947)
<i>Succisa pratensis</i>	2	" "
<i>Dipsacus fullonum</i>	2	" "
<i>Galinsoga parviflora</i>	2	(Lawalrée, 1948)
<i>Chrysanthemum leucanthemum</i>	2	" "
<i>Myrica californica</i>	1-3	(Reeve, 1948)
<i>Cornus californica</i>	1-3	" "
<i>C. nuttallii</i>	1-3	" "
<i>C. rostrata</i>	1-3	" "
<i>Castanopsis californica</i>	3-4	" "
<i>Lithocarpus californica</i>	3-4	" "
<i>Quercus kelloggii</i>	3-4	" "
<i>Salix laevigata</i>	2	" "
<i>Ananas comosus</i>	1 (?)	(Krauss, 1948)
<i>Lupinus albus</i>	1-2	(Ball, 1949)
<i>Dianthera americana</i>	2-3	(Sterling, 1949b)
<i>Glycine max</i>	2	(Sun, 1950)

DISCUSSION

Many authors have pointed out small differences that exist between shoot apices of various genera, between shoot apices of the same species, and between zones in a single apex, but the equally important consideration of similarities has been neglected. A student of plant anatomy can find only a series of isolated, detailed, and seemingly unrelated descriptions of shoot apices in the literature. If useful comparisons are to be made and if there is to be an intelligent selection of research materials in the future, an over-all pattern of what is known must first be perceived. The author has attempted, by neglecting minor details of difference, to outline such a pattern (table 1).

If it is true that in most individuals the gene complement of all cells of vegetative organs is identical, it appears fairly certain that some of the types of shoot apex organization described are more positively determined by heredity in some species than in others. In some species gene control is sufficiently unstable and the heredi-

⁸In spite of references to a cambium-like zone in the shoot apex of *Heracleum* by others, the present author could not find in Majumdar's paper a satisfactory description confirming the existence of such a zone.

tary limits are sufficiently broad so as to occasionally allow external and internal environmental factors to exert the determining influence. *Chrysanthemum morifolium*, *Zea mays* and several other monocots, *Taxodium distichum*, *Selaginella martensii*, *S. kraussiana*, *S. poulteri*, *S. gracilis*, *Lycopodium phlegmaria*, *Isoetes hystrix*, *Danaea alata*, *D. nodosa*, *D. simplicifolia*, *Kaulfussia aesculifolia*, *Angiopteris evecta*, and *Marattia alata*, are examples of plants in which the physiological state within the shoot apex may be sufficiently altered by the environment to result in different types of shoot apex zonation (1) in different apices on the same plant or (2) in different stages of ontogeny in the same shoot apex. These variations have been noted previously in this paper and will therefore not be described again. Differences in contour of shoot apices of the same plant, differences in dimensions of the shoot during different stages in the plastochrone, and differences in the number of mantle layers (if present) of shoot apices of the same plant have been noted by many authors (Schmidt, 1924; Louis, 1935; Cross and Johnson, 1941;

TABLE 1
A summary of the distinguishing features of the principal types of vegetative shoot apex organization in vascular plants.

Characteristic Features	Type I Fern	Type II Transition	Type III Lycopodium	Type IV Ginkgo	Type V Abies-Cryptomeria	Type VI Opuntia	Type VII Usual Angiosperm
Single Apical Cell.....	*
2-5 Apical Cells.....	*
Surface Meristem (S) (both anti- and periclinical divisions in surface row).....	*	*	*
Mantle (M) (anticlinal divisions only in surface layer(s)).....	*	*
Central Mother Cells (MO).....	*	*
Cambium-Like Zone (C).....	*	*
Sub-Apical Initials (SA).....	*	*
Central Meristem (CM).....	*	*	*	*	*
Peripheral Meristem (P).....	*	*	*	*	*

Engard, 1944; Reeve, 1948; Popham and Chan, 1950; and others). Complexity of the zonal pattern or volume of zones or both may be considerably reduced in the early phase of the plastochrone (time of minimal size of the shoot apex) in *Torreya californica* (Kemp, 1943), *Abies concolor* (Korody, 1937), *Gnetum gnemon* (Johnson, 1950) and *Chrysanthemum morifolium* (Popham and Chan, 1950). These differences are probably not controlled completely by heredity.

In the light of the facts cited above, it behooves the researcher to examine many shoot apices from many locations on the same plant and on different plants of the same species, as well as shoot apices exhibiting different stages in the plastochrone before he makes any definite statements regarding the structure of the shoot apex of any particular plant.

If the reader will peruse the plant names listed for each type of shoot apex organization, little doubt can exist that heredity is an important factor in the determination of shoot apex organization and the growth pattern. It will be seen that there is a phylogenetic trend toward reduction of the number of periclinal and oblique cell divisions at the surface of the apex. The trend in the plant

kingdom appears to be from (1) a single apical cell to (2) a few apical cells to (3) many cells dividing anticlinally, periclinally, and obliquely, arranged throughout a very irregular surface row to (4) a very few cells dividing periclinally accompanied by many cells dividing anticlinally, arranged throughout a regular surface layer to (5) a very few periclinally dividing cells at the summit of the surface layer to (6) all cells of the surface layer dividing anticlinally.

It is rather disconcerting to find (1) that although a diversity of types of shoot apex organization exists, most of the species exhibit basic similarities in that there is a rather uniform development of protoderm, procambium, and ground meristem back of the apex proper and (2) that plants such as *Zea*, *Washingtonia*, and *Carya* having such dissimilar tissue organization in the older portions of the stem show a similar shoot apex structure (Type VII). From these examples and many others that could be cited, one is forced to infer that stem structure is not obviously (if at all) related to shoot apex structure.

Whether inconsistencies, such as a monocot (*Livistona*) and a composite (*Chrysanthemum*) exhibiting the same type (Type VI) of shoot apex organization, (1) are only apparent, due to inaccurate or insufficient observations or (2) are real, due to the fact that the same progression, ending in the presence of the zone of cambium-like cells, reappears in various phylogenetic lines of higher plants, remain unanswered questions.

It will be noted that no angiosperm shoot apex has been described in which periclinal divisions regularly or frequently occur in the surface layer of cells. In other words, all angiosperm apices thus far studied exhibit at least one true tunica layer (Sterling, 1944). Only two gymnosperms, (*Araucaria brasiliana* and *Sciadopitys verticillata* (Strasburger, 1872), are presumed to exhibit no periclinal divisions in the surface layer. For this reason a reinvestigation of these species is in order.

It should be emphasized that the surface cloak of cells in Type III does not present the appearance of a *regular layer*. Periclinal and oblique divisions and subsequent cell enlargement occur too frequently at irregular intervals and too extensively in the surface cloak to allow a stratified appearance. In Types IV through VII this is not the case. Even though periclinal divisions occur in the surface cloak of cells in types IV and V, they are so infrequent (and even then, in some species, they are restricted to the few summit cells of the cloak) that a definitely stratified appearance results. No periclinal divisions occur in the surface layer in Types VI and VII. These considerations are important to an understanding of growth at the shoot apex. In Types IV through VII the surface layer of cells is of little (Types IV and V) or no (Types VI and VII) importance in the elongation of the shoot except insofar as extension of the epidermis is concerned. In species having Type III shoot apex organization, the surface cloak of cells is of paramount importance in shoot elongation.

After considering the facts, it is seen that the term *tunica* if strictly defined, allowing no periclinal divisions in its layers except during leaf and bud initiation, may be used only in describing shoot apices exhibiting Types VI and VII organization. It may be applied to one or more layers of cells. There may be, however, other subjacent layers in which only *occasional* periclinal divisions occur. These layers for all practical considerations should also be thought of as contributing little to extension growth of the shoot as a whole. Since the term *tunica* connotes a strict usage to some workers and a loose usage, allowing few or many periclinal divisions, to others, its usefulness in accurately describing growth relations at the shoot apex is questionable. It is primarily for this reason that the term *mantle* has been used in describing zonal organizations. The mantle is thought of as including all layers at the summit of the apex in which anticlinal divisions are sufficiently frequent to result in the perpetuation of definite cell layers. The mantle therefore accounts for extension growth of its own layers primarily and only incidentally accounts for the perpetuation of underlying growth zones.

Use of the term *corpus* has been avoided because it was not found useful in presenting an accurate concept of the part played by cells underlying the "*tunica*." If the term *corpus* were used, it could be applied logically only to types VI and VII in which a true "*tunica*" is present. Therefore it would include two zones in which cell divisions are not rapid (the central mother cells and sub-apical initials), and four types of active meristems (1) stratified layers of cells underlying the *tunica* in many species in which divisions are mostly anticlinal, (2) the cambium-like zone, (3) the central meristem, and (4) the peripheral meristem. It seems to the author that the term *corpus* when used to include such a heterogeneous assemblage of growth zones is likely to convey a confused, over-simplified and erroneous concept of shoot growth, if indeed it conveys any at all.

The term *central meristem* was chosen in lieu of rib meristem since shoot apices of some species (*Ephedra altissima*, Gifford, 1943, and others) do not always exhibit pith forerunner cells in distinct longitudinal tiers or tapered filaments. In some species, such as *Heracleum*, the file (rib) meristem does not appear in the shoot apex above the last leaf primordium (Majumdar, 1945).

SUMMARY

1. Seven principal types of shoot apex organization have been described for vascular plants. The major differences and similarities are summarized in table 1. The growth patterns of each of these types are summarized in figure 1. Shoot apex Types I, II, and III have been found to exist only among the pteridophytes, with one exception (*Cycas revoluta*—Type III). Types IV and V reportedly exist only in gymnosperm shoot apices while Types VI and VII occur in shoot apices of angiosperms only, with two doubtful exceptions (*Araucaria brasiliiana* and *Sciadopitys verticillata*—both Type VII).

2. Since different types of organization appear in shoot apices of the same individual plant, and since the same type of organization occurs in shoot apices of plants in different genera, it follows that differences in shoot apex organization do not necessarily cause external differences in form.

3. Since different types of organization appear in shoot apices of the same individual, species, and genus of plants, it follows that differences in shoot apex structure are seldom of taxonomic value.

4. Shoot apex organization types may be of some value in broad phylogenetic studies. The following stages mark a trend in the organization of shoot apices from lower to higher vascular plants:

- a. A single apical cell.
- b. A few (2-5) apical cells.
- c. A surface row of many irregularly elongate cells dividing anticlinally, periclinally, and obliquely.
- d. A stratified surface layer of cells, many dividing anti-clinally and few dividing periclinally, located at the summit and along the flanks of the apex.
- e. A stratified surface layer of cells in which anticlinal divisions are most frequent and periclinal divisions are restricted to the summit of the apex only.
- f. One or more stratified surface layers of cells in which all divisions are anticlinal.

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